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RESEARCH PAPERS

# Physiological and Biochemical Responses in Novel Eggplant Lines under Heat Stress Condition

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**Abstract**—Eggplant (*Solanum melongena* L.), an important Solanaceous vegetable, is significantly affected by heat stress, particularly during the reproductive stage, leading to reduced fruit set, pollen degeneration, and oxidative damage. This study evaluated ten eggplant genotypes of which five reported to be tolerant and five susceptible for heat stress, based on physiological and biochemical responses under high-temperature stress (summer season) and compared them with normal growing conditions (rainy season). Heat stress resulted in a significant decline in relative water content, total chlorophyll content, chlorophyll fluorescence, and membrane stability index, with susceptible genotypes like G-131 and EC-368225 exhibiting the highest reduction. Canopy temperature was significantly higher in summer, while tolerant genotypes (Pusa Shyamla, Pant Samrat) exhibited better transpirational cooling. Proline accumulation, a stress tolerance bio-chemical, was elevated in tolerant genotypes. There was increased production of hydrogen peroxide and malondialdehyde in summer season crop and the rate of increase was higher in susceptible genotypes. Antioxidant enzyme activity, including superoxide dismutase and catalase, was higher in tolerant genotypes, indicating their role in scavenging reactive oxygen species. Hierarchical clustering and principal component analysis effectively differentiated heat-tolerant and susceptible genotypes. The study highlights the physiological and biochemical mechanisms underlying heat tolerance in eggplant, providing insights into selecting resilient genotypes with higher anthocyanin for breeding programs aimed at climate adaptation.

**Keywords:** *Solanum melongena*, eggplant, heat stress, physiological changes, antioxidant enzymes

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## INTRODUCTION

Climate change including temperature variations affects the growth and yield of crop plants [1]. Vegetable crops are more vulnerable to climate change among horticultural crops [2]. Heat stress (HS) caused by high temperature is one of the most destructing environmental stress limiting the growth and yield of the plant and also its geographical distribution in many parts of the world. Temperature plays a crucial role in plant growth, development, reproduction, and yield [3, 4]. But the extreme environmental conditions cause reduction in growth of plants [5]. The Fourth Assessment of the Intergovernmental Panel on Climatic Change (IPCC) forecasted that the global average temperature will be increased between 1.8 and 4°C in 2100 [6]. Temperature stress hinders crop growth which finally has negative financial impact. HS, due to increased temperature, causes a series of changes in plants at the morpho-anatomical, physiological, biochemical and molecular levels resulting in a drastic loss of economic yield [7]. HS causes various physiological changes in plants, such as scorching of leaves and stems, leaf abscission and senescence, shoot and root growth inhibition or reduction in number of flowers, pollen tube growth and pollen in-fertility, fruit damage, leading to catastrophic loss of crop yield [8–10]. HS also affects the photosynthesis, respiration, water relations, membrane stability, and modulates levels of hormones and primary and secondary metabolites [10]. The disturbance in metabolic homeostasis leads to the accumulation of toxic by-products, such as reactive oxygen species (ROS) [3]. To survive or maintain the steady-state balance of metabolic processes under HS, plants

**Table 1.** Plant materials used and their source in the present study

| Sample n. | Genotypes | Source |
|---|---|---|
| 1 | Guhala Chatua Local | Orrisa |
| 2 | Pusa Shyamla | ICAR-IARI, New Delhi |
| 3 | Pant Samrat | GBPUA&T, Uttarakhand |
| 4 | DBL-08 | ICAR-IARI, New Delhi |
| 5 | Pusa Ankur | ICAR-IARI, New Delhi |
| 6 | G-43 | ICAR-IARI, New Delhi |
| 7 | G-23 | ICAR-IARI, New Delhi |
| 8 | EC-368225 | ICAR-NBPGR, New Delhi |
| 9 | G-131 | ICAR-IARI, New Delhi |
| 10 | Pusa Upkar | ICAR-IARI, New Delhi |

reprogram their transcriptome, proteome, metabolome, and lipidome, thereby adjusting their composition of certain transcripts, proteins, metabolites and lipids [3]. Many heat shock proteins (*e.g.* HSP100, HSP90, HSP70, HSP60, HSP40, and the small HSP (sHSP) are accumulated in plants to mitigate the adverse effect of HS on plant metabolism [11–14].

Eggplant (*Solanum melongena* L.) also known as brinjal and aubergine, is one of the non-tuberiferous Solanaceous crop, having its centre of diversity between India and Indonesia [15]. Due to its wide range of available diversity, it is known as king of vegetables in India [16]. Among the several abiotic stress, heat stress is given more attention due to their role on hindering growth and development of crop more specifically in tropical countries. A moderately warm and long growing season is desirable for eggplant cultivation. The ideal temperature for its growth is 20–30°C, but during the summer months, when the temperature remains above 35°C, this affects the plant growth and, subsequently, yields [17]. Rainy season is the main growing season for eggplant cultivation in north India where fruiting occurs during September–December. During summer season, eggplant can be grown as off-season vegetable in northern plains, which fetch premium prize in the market [18]. The optimum temperature requirement for fruit set in eggplant is 18–21°C and there has many number of cultivars available to grow in autumn-winter season [19] but when day and night temperature exceeds 35°C respectively there is drastic reduction in fruit set, drying of stigmatic fluid, pollen degeneration, low germination of pollen and lack of fertilization with lower fruit weight [20, 21]. Also in eggplant, high temperature conditions lead to substantial loss in plant growth productivity, fruit growth and hinder reproductive development [4, 22, 23]. During summer season, which is the main heat stress season, especially in Northern India, the temperatures may rise up to 45/30°C (day/night), which might have an adverse effects on their performance and potential yields. Their responses to heat stress and the mechanisms underlying heat sensitivity of eggplant crop at reproductive stage are not known so far, which formed the bases of the present study.

The crop plants generally overcome stress by scavenging reactive or toxic oxygen species induced by stress, which includes hydrogen peroxide ($H_2O_2$), hydroxyl radical and superoxide radical. Catalases and peroxidases are major enzyme system for removal of $H_2O_2$. These reactive oxygen species can damage proteins, chlorophylls, membrane lipids, and nucleic acids [24, 25]; protective antioxidants are necessary to overcome these damages. Hence, the physiological and biochemical study of heat tolerant and heat susceptible eggplant genotypes was carried out in this experiment. It is the need of the hour to get maximum yield to fill the need of increasing population of the world which is expected to be more than 12 billion in 2100 [26]. The aim of this study was to determine the heat stress impact on various physiological and biochemical parameters in the leaves. For this purpose, the eggplant lines were grown during spring summer season where temperature remains above normal. Additionally, the plants were also tested under normal growing season (rainy season) to characterize the stressful temperatures and to minimize the confounding effects of any other external factors which might influence the results in outdoor conditions.

## MATERIALS AND METHODS

The experiment was carried out at Division of Vegetable science, ICAR-Indian Agricultural Research Institute, New Delhi, India. For the current study 10 eggplant genotypes were used, five of which were identified as heat stress-tolerant and five as susceptible, based on yield data obtained by Santhiya et al. [27]. The genotypes were grown in the field for two years in 2018 and 2019 (Table 1). In each year, the crop was raised for two season, i.e., under heat stress condition in summer (March–June), when day/night temperatures at the flowering and fruiting stage were 40/26.2°C (transplantation was performed so that reproductive stage coincided with heat stress periods), and under normal condition, i.e., during the rainy season (July–October), when day/night temperatures at flowering and fruiting stage were 32.4/17.2°C. The minimum and maximum temperature for the summer and rainy seasons of 2018 and 2019 are represented in graphical format (Figs. 1a, 1b). Ten eggplant genotypes were tested for different physiological and biochemical parameters in leaf samples collected from 5 randomly selected plants of the tolerant and susceptible genotypes in both years of evaluation. Besides, three fruits were harvested from each line at the edible maturity stage for nutritional quality analysis. All the crop cultivation practices were followed as per the standard package of practices.

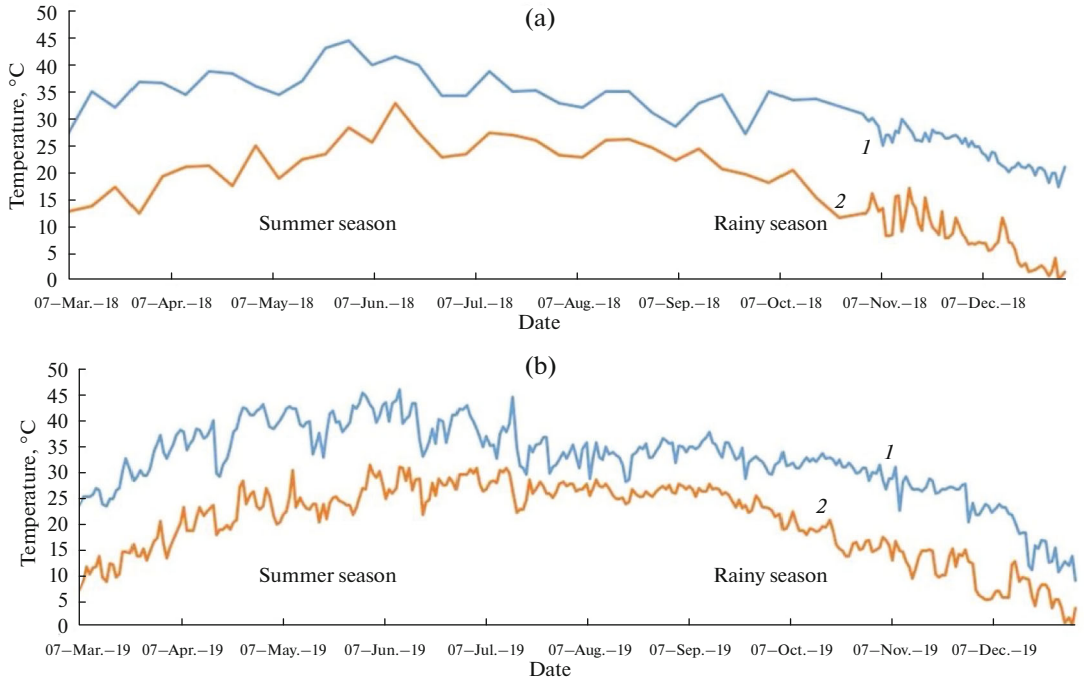


**Fig. 1.** (a) Minimum and maximum temperature of summer and rainy season of 2018 is represented in graphical format. (b) Minimum and maximum temperature of summer and rainy season of 2019 is represented in graphical format. (*1*) maximum temperature; (*2*) minimum temperature.

### *Physiological Parameters*

**Relative water content (RWC) of leaf.** Relative water content was measured using a method described by Weatherley [28]. Fully expanded whole leaf is taken from 5 plants of each genotype. Initially the fresh weight (FW) of the leaf is measured. Then the samples are placed in Petri dish filled with distilled water for 4 h, these leaves are taken and the respective turgid weight (TW) is measured. After this, blotting paper is used to remove the excess water from the turgid leaves. Then, the respective leaves are packed in butter paper cover and subjected for oven drying at 65°C for 48 h. The oven dried sample was taken out and their respective dry weight (DW) is measured. Relative water content is measured using the following Eq. (1):

$$\text{RWC, \%} = \left[(\text{FW} - \text{DW})/(\text{TW} - \text{DW})\right] \times 100. \quad (1)$$

**Total chlorophyll content.** Total chlorophyll (Chl) was estimated using Hiscox method (DMSO method) which was given by Hiscox and Israelstam [29]. Finely chopped fresh leaves weighing 50 mg were taken in a glass test tube, to which 10 mL of DMSO is added. These tubes were placed in an oven, covered with aluminum foil to prevent evaporation, and incubated at 65°C for 4 h. After that, the sample was cooled to room temperature and the absorbance was recorded at 663 and 645 nm against DMSO as a blank solution in a spectrophotometer (Eppendorf, USA). The total Chl level was then estimated using Eq. (2) given by Arnon [30]:

$$\text{Total Chl, mg/g FW} = \left[\left((20.2A_{645} + 8.02A_{663})/1000\right)w\right]v, \quad (2)$$

where, $w$ is weight of the sample; $v$ is final volume of the extract.

**Canopy temperature measurement.** Canopy temperature (°C) of selected genotypes was measured using infrared thermography (Fluke 62 MAX Hand-Held Infrared Thermometer; Fluke, UK).

**Chlorophyll fluorescence.** Chlorophyll fluorescence ($F_v/F_m$) which informs about performance of photosynthesis and functioning of photosynthetic apparatus in green plant tissue was measured using portable modulated chlorophyll fluorometer (OPTI-Sciences, Inc., USA). The plants were dark-adapted for a minimum of 30 min prior to measurement to ensure accurate assessment of the maximum potential quantum efficiency of Photosystem II.

### *Biochemical Parameters*

**Hydrogen peroxide ($H_2O_2$) content**. $H_2O_2$ was estimated spectrophotometrically by reaction with potassium iodide as described by Alexieva et al. [31]. 200 mg of leaf sample was ground using liquid nitrogen mixed with 4 mL of trichloroacetic acid (TCA), and the homogenate was centrifuged at 12000 rpm for 20 min at 4°C. The reaction mixture consisting of 0.5 mLof

TCA extract, 2 mL of 1 mM KI, and 0.5 mL of 100 mM phosphate buffer was kept in dark for 1 h. The absorbance of the reaction mixture was then measured at 390 nm against TCA as a blank sample. The level of $H_2O_2$ was calculated using Eq. (3):

$$H_2O_2, \mu mol/g\ FW = CV/FW, \quad (3)$$

where $C$ is concentration of $H_2O_2$ obtained from the standard curve (μmol/mL or μM); $V$ is total volume of the extract (mL); FW is fresh weight of the tissue sample (g).

**Malondialdehyde content (MDA)**. MDA, as an indicator of lipid peroxidation, was estimated using the TBARS assay as described by Heath and Packer [32]. Leaf samples (200 mg) were ground in liquid nitrogen and homogenized in 4 mL of 0.1% TCA. The homogenate was centrifuged at 12000 rpm for 10 min at 4°C. The supernatant (0.1 mL) was mixed with 4 mL of 10 mM thiobarbituric acid (TBA) in 20% TCA and incubated at 95°C for 30 min. After cooling, the mixture was centrifuged at 10000 rpm for 10 min and absorbance was measured at 532 and 600 nm. The amount of MDA was calculated using the following Eq. (4):

$$TBARS, \mu g/g\ FW = FW \times A_{532} \times \varepsilon, \quad (4)$$

where ε is extinction coefficient 155 $mM^{-1}\ cm^{-1}$, FW is fresh weight of sample.

**Proline estimation.** Proline content was determined according to Bates et al. [33]. Fresh leaf tissue (0.5 g) was homogenized in 5 mL of 3% sulphosalicylic acid, and the homogenate was filtered through Whatman No. 1 paper. The reaction mixture contained 2 mL of filtrate, 2 mL of glacial acetic acid, and 2 mL of 2% acid-ninhydrin solution. After incubation at 100°C for 30 min, the tubes were cooled and 6 mL of toluene was added. The upper phase containing chromophore was collected, and its absorbance was measured at 520 nm. The proline concentration was calculated using a standard curve for L-proline and expressed as μmol/g FW [33].

**Antioxidant enzymes extraction and assay.** Enzyme extracts were prepared from 1.0 g of leaf tissue frozen in liquid nitrogen and ground in 10 mL of extraction buffer (0.1 M phosphate buffer, pH 7.5, supplemented with 0.5 mM EDTA). The homogenate was centrifuged at 15000 *g* for 20 min at 4°C, and the supernatant was used to measure antioxidant enzymes activities.

**Superoxide dismutase activity (SOD).** SOD activity was measured based on the inhibition of the photochemical reduction of nitroblue tetrazolium (NBT) [34]. The reaction mixture was illuminated under a 15 W fluorescent lamp for 15 min, and absorbance was recorded at 560 nm. One unit of SOD activity was defined as the amount of enzyme required to inhibit NBT reduction by 50%, calculated using Eq. (5):

$$SOD, U/min\ mg\ protein = (A_{560} - B_{560})/C_{560}, \quad (5)$$

where $A$ is depicts the absorbance of control samples, $B$ represents the absorbance of extracted samples, and $C$ represents the absorbance of the control/buffer.

**Catalase activity.** Catalase activity was determined by monitoring the decomposition of $H_2O_2$ as a decrease in absorbance at 240 nm over 1 min. The amount of decomposed $H_2O_2$ was calculated using a standard curve, and enzyme activity was expressed as μmol $H_2O_2$/g FW/min.

**Membrane stability index (MSI)**. MSI of cell was determined by measuring electrolyte leakage. Leaf samples (100 mg) were incubated in 10 mL $dH_2O$ at 40°C for 30 min, and the electrical conductivity ($C_1$) was recorded. The samples were then heated at 95°C for 10 min, and the electrical conductivity ($C_2$) was measured using Eq. (6):

$$MSI, \% = (1 - C_1/C_2) \times 100. \quad (6)$$

**Total anthocyanin estimation (TAC).** TAC was estimated in fresh eggplant peels according to the method of Giusti and Wrolstad [35]. Fresh eggplant peels (5.0 g) were homogenized in 10 mL of acidified ethanol (95% ethanol : 1 N HCl, 85 : 15; v/v) and kept at 4°C overnight. The mixture was filtered, and the final extract volume was adjusted to 100 mL with $dH_2O$. Aliquots of the extract were appropriately diluted with a buffer solution of potassium chloride (pH 1.0) and sodium acetate (pH 4.5). Absorbance was recorded at 520 nm and 700 nm against the corresponding buffer as blank. The concentration of monomeric anthocyanins was calculated using the following Eq. (7).

$$TAC, mg/L = [(A_{520} - A_{700})\,pH_{1.0} - (A_{520} - A_{700})\,pH_{4.5}] \times MWDF \times 10^3/(\varepsilon l), \quad (7)$$

where MW is 449.2 g/mol (cyanidin-3-glucoside), ε is coefficient 26900 L $mol^{-1}\ cm^{-1}$, DF is dilution factor, l is path length equal 1 cm.

**Statistical analysis**. Augmented Hierarchical Cluster Analysis (AHCA) was employed to investigate the grouping of genotypes based on similarities and dissimilarities in quantitative pooled data of two years (2018 and 2019) utilizing the modeling methods of R package. Principal Component Analysis (PCA), a method for dimensionality reduction, was also performed using R 4.4.2 package.

## RESULTS

### *Relative Water Content, Total Chlorophyll Content and Chlorophyll Fluorescence*

The relative water content (RWC), total chlorophyll content, and chlorophyll fluorescence of both summer and rainy season and their seasonal difference are given in Table 2. RWC was found higher in rainy season crop compared to summer season crop invari-

**Table 2.** Relative water content, total chlorophyll content and chlorophyll fluorescence of summer and rainy season and their seasonal difference (Pooled data)

| Genotypes | RAW, % | | | Total Chl, mg/g FW | | | $F_v/F_m$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | summer | rainy | seasonal difference | summer | rainy | seasonal difference | summer | rainy | seasonal difference |
| Guhala Chatua Local | 54.17 ± 3.07 | 63.52 ± 4.38 | +9.35 | 1.41 ± 0.05 | 1.71 ± 0.13 | +0.30 | 0.69 ± 0.04 | 0.74 ± 0.02 | +0.05 |
| Pusa Shyamla | 51.15 ± 6.64 | 57.00 ±7.64 | +5.85 | 1.14 ± 0.04 | 1.31 ± 0.00 | +0.17 | 0.65 ± 0.03 | 0.70 ± 0.04 | +0.05 |
| Pant Samrat | 57.20 ± 1.51 | 66.52 ± 0.65 | +9.32 | 1.88 ± 0.03 | 2.14 ± 0.06 | +0.26 | 0.68 ± 0.03 | 0.70 ± 0.05 | +0.02 |
| DBL-08 | 52.65 ± 1.93 | 61.29 ± 1.33 | +8.64 | 2.0 ± 0.07 | 2.88 ± 0.13 | +0.88 | 0.61 ± 0.02 | 0.71 ± 0.005 | +0.10 |
| Pusa Ankur | 52.74 ± 1.95 | 64.35 ± 2.15 | +11.61 | 1.33 ± 0.07 | 1.80 ± 0.027 | +0.47 | 0.65 ± 0.01 | 0.68 ± 0.05 | +0.03 |
| G-43 | 44.62 ± 3.62 | 58.52 ± 1.79 | +13.90 | 1.22 ± 0.05 | 1.96 ± 0.22 | +0.73 | 0.55 ± 0.06 | 0.68 ± 0.08 | +0.13 |
| G-23 | 47.61 ± 0.91 | 60.52 ± 2.65 | +12.90 | 0.85 ± 0.43 | 1.59 ± 0.36 | +0.73 | 0.62 ± 0.02 | 0.71 ± 0.03 | +0.09 |
| EC-368225 | 51.32 ± 0.92 | 64.26 ± 1.23 | +12.94 | 1.09 ± 0.01 | 1.80 ± 0.04 | +0.72 | 0.59 ± 0.08 | 0.67 ± 0.07 | +0.08 |
| G-131 | 43.63 ± 2.22 | 60.98 ± 6.03 | +17.34 | 0.83 ± 0.02 | 1.78 ± 0.03 | +0.95 | 0.47 ± 0.02 | 0.58 ± 0.04 | +0.11 |
| Pusa Upkar | 48.14 ± 3.11 | 61.16 ± 0.84 | +13.02 | 0.72 ± 0.12 | 2.01 ± 0.24 | +1.30 | 0.53 ± 0.10 | 0.70 ± 0.01 | +0.16 |
| CD at 5% | 3.05 | 2.05 | – | 0.30 | 0.29 | – | 0.05 | 0.03 | 1.20 |
| CV% | 8.49 | 4.65 | – | 34.30 | 21.85 | – | 11.60 | 6.17 | 6.82 |

**Table 3.** Canopy temperature and membrane stability index of summer and rainy season and their seasonal difference (Pooled data)

| Genotypes | Canopy temperature, °C | | | MSI, % | | |
|---|---|---|---|---|---|---|
| | Summer | Rainy | Seasonal difference | Summer | Rainy | Seasonal difference |
| Guhala Chatua Local | 32.33 ± 1.25 | 25.20 ± 1.00 | −7.13 | 72.38 ± 1.36 | 83.14 ± 1.98 | +10.76 |
| Pusa Shyamla | 30.50 ± 0.79 | 25.73 ± 1.81 | −4.77 | 73.03 ± 1.07 | 80.93 ± 5.21 | +7.90 |
| Pant Samrat | 30.70 ± 0.26 | 23.73 ± 0.85 | −6.97 | 74.59 ± 1.68 | 81.21 ± 5.55 | +6.62 |
| DBL-08 | 32.02 ± 0.42 | 27.70 ± 1.51 | −4.32 | 75.21 ± 5.18 | 84.02 ± 2.07 | +8.82 |
| Pusa Ankur | 31.97 ± 0.64 | 26.43 ± 0.40 | −5.53 | 76.66 ± 0.17 | 82.99 ± 0.96 | +6.33 |
| G-43 | 34.37 ± 0.92 | 23.10 ± 0.88 | −11.27 | 63.81 ± 4.90 | 77.93 ± 1.50 | +14.12 |
| G-23 | 31.37 ± 0.25 | 23.93 ± 0.92 | −7.43 | 67.17 ± 6.34 | 79.94 ± 3.15 | +12.77 |
| EC-368225 | 32.17 ± 0.25 | 22.10 ± 0.79 | −10.07 | 67.08 ± 1.08 | 81.92 ± 2.47 | +14.84 |
| G-131 | 33.87 ± 0.30 | 23.66 ± 1.76 | −10.20 | 63.00 ± 8.05 | 82.94 ± 1.76 | +19.94 |
| Pusa Upkar | 35.53 ± 1.01 | 25.27 ± 1.15 | −10.27 | 62.84 ± 3.01 | 81.86 ± 2.34 | +19.01 |
| CD at 5% | 1.16 | 1.20 | – | 3.85 | 1.28 | – |
| CV% | 4.99 | 6.82 | – | 7.73 | 2.19 | – |

ably of the genotypes. In summer season (heat stress condition), the percentage of RWC ranged from 43.63 to 57.2%, with a mean value of 50.32%. The maximum RWC was recorded in Pant Samrat (57.2%) and minimum was in G-131 (43.63%). In rainy season, the RWC ranged from 57% (Pusa Shyamla) to 66.52% (Pant Samrat), with a mean value of 61.81%. The highest (+17.34) seasonal difference was observed for G-131, which was a susceptible genotype due to a drastic reduction of RWC under heat stress condition.

The maximum Chl content was observed for Guhala Chatua Local (1.41 mg/g FW) and the minimum in the Pusa Upkar (0.72 mg/g FW) during the summer season, with a mean value of 1.24 mg/g FW. In case of rainy season, the maximum Chl content was observed in the DBL-08 (2.88 mg/g FW) and minimum in the Pusa Shyamla (1.31 mg/g FW) with a mean value of 1.89 mg/g FW.

The average chlorophyll fluorescence, indicating of PSII function, was highest in the Guhala Chatua local (0.69) during the summer, while the average Chl fluorescence during the monsoon season was 0.68, as shown in Table 2.

### *Canopy Temperature and Membrane Stability Index*

In summer, canopy temperatures range from 30.5°C (Pusa Shyamla) to 35.53°C (Pusa Upkar), with a mean value of 32.48°C, whereas during the rainy season, canopy temperatures range from 22.1°C (EC-368225) to 27.7°C (DBL-08) with a mean value of 24.68°C.

The membrane stability index (MSI), measured as electrolyte leakage, in the summer season ranged from 62.84% in Pusa Upkar to 76.66% in Pusa Ankur, with a mean value of 69.57%. During the rainy season the MSI ranges from 77.93 to 84.02% with an average value of 81.67%. The lowest value was in G-43 (77.93%) and the highest in DBL-08 (84.02%). The largest seasonal difference (+19.94) was observed for G-131. The canopy temperature and MSI in both the rainy and summer seasons, as well as their seasonal difference, are presented in Table 3.

### *Proline, $H_2O_2$ and Malondialdehyde Content*

The proline, $H_2O_2$, and MDA contents in summer and rainy seasons are presented in Table 4. In our study, proline content was high in the tolerant genotype Pusa Shyamla (1.87 μmol/g FW) compared to the susceptible genotypes G-23 in summer season. During the rainy season, proline content ranged from 0.02 to 0.18 μmol/g FW, with a mean value of 0.073 μmol/g FW.

The amount of $H_2O_2$, a measure of oxidative damage, ranges from 1.7 to 3.44 μmol/g FW, with an average value of 2.61 μmol/g FW. The highest was observed in EC-368225 (3.44 μmol/g FW), and the lowest in Pusa Shyamla (1.7 μmol/g FW) in summer season. The $H_2O_2$ content during monsoon season was minimum in Pusa Ankur (0.29 μmol/g FW) and maximum in Guhala Chatua Local (2.03 μmol/g FW), with a mean value of 1.24 μmol/g FW.

MDA, the product of lipid peroxidation was ranged from 0.007 to 0.026 with mean value of 0.015 in summer season, were the lowest being found in Pusa Shyamla (0.007 μg MDA/g FW) and Pusa Ankur (0.007 μg MDA/g FW). In rainy season, the MDA range was from 0.003 μg MDA/g FW in Pusa Ankur to 0.008 μg MDA/g FW in G-131, with the mean value of 0.0054 (Table 3).

**Table 4.** Proline, $H_2O_2$, and malondialdehyde of summer and rainy season and their seasonal difference (Pooled data)

| Genotypes | Proline, µmol/g FW | | | $H_2O_2$, µmol/g FW | | | MDA, µg /g FW | | |
|---|---|---|---|---|---|---|---|---|---|
| | summer | rainy | seasonal difference | summer | rainy | seasonal difference | summer | rainy | seasonal difference |
| Guhala Chatua Local | 1.64 ± 0.22 | 0.13 ± 0.02 | −1.51 | 2.98 ± 0.07 | 2.03 ± 0.26 | −0.96 | 0.014 ± 0.003 | 0.005 ± 0.003 | −0.009 |
| Pusa Shyamla | 1.87 ± 0.02 | 0.02 ± 0.005 | −1.85 | 1.70 ± 0.25 | 1.49 ± 0.18 | −0.20 | 0.000 ± 0.001 | 0.005 ± 0.003 | −0.002 |
| Pant Samrat | 1.69 ± 0.01 | 0.03 ± 0.01 | −1.67 | 2.32 ± 0.23 | 1.47 ± 0.15 | −0.85 | 0.009 ± 0.005 | 0.007 ± 0.004 | −0.002 |
| DBL-08 | 1.57 ± 0.08 | 0.07 ± 0.01 | −1.49 | 2.57 ± 0.27 | 2.01 ± 0.78 | −0.56 | 0.012 ± 0.009 | 0.006 ± 0.003 | −0.005 |
| Pusa Ankur | 1.68 ± 0.13 | 0.04 ± 0.01 | −1.64 | 2.02 ± 0.04 | 1.01 ± 0.31 | −1.00 | 0.007 ± 0.006 | 0.003 ± 0.002 | −0.004 |
| G-43 | 0.86 ± 0.03 | 0.08 ± 0.04 | −0.78 | 2.65 ± 0.23 | 0.87 ± 0.28 | −1.78 | 0.016 ± 0.001 | 0.005 ± 0.004 | −0.011 |
| G-23 | 0.52 ± 0.06 | 0.03 ± 0.00 | −0.48 | 3.14 ± 0.24 | 1.13 ± 0.26 | −2.01 | 0.017 ± 0.006 | 0.005 ± 0.003 | −0.013 |
| EC-368225 | 0.81 ± 0.06 | 0.13 ± 0.06 | −0.68 | 3.44 ± 0.55 | 0.65 ± 0.05 | −2.79 | 0.023 ± 0.013 | 0.006 ± 0.005 | −0.017 |
| G-131 | 0.66 ± 0.08 | 0.18 ± 0.05 | −0.47 | 2.88 ± 0.22 | 1.41 ± 0.30 | −1.47 | 0.026 ± 0.002 | 0.008 ± 0.005 | −0.019 |
| PusaUpkar | 0.67 ± 0.28 | 0.02 ± 0.01 | −0.65 | 2.46 ± 0.55 | 0.29 ± 0.12 | −2.17 | 0.021 ± 0.006 | 0.004 ± 0.002 | −0.017 |
| CD at 5% | 0.38 | 0.04 | – | 0.37 | 0.39 | – | 0.004 | 0.001 | – |
| CV% | 44.48 | 76.96 | – | 20.00 | 45.23 | – | 43.83 | 26.47 | – |

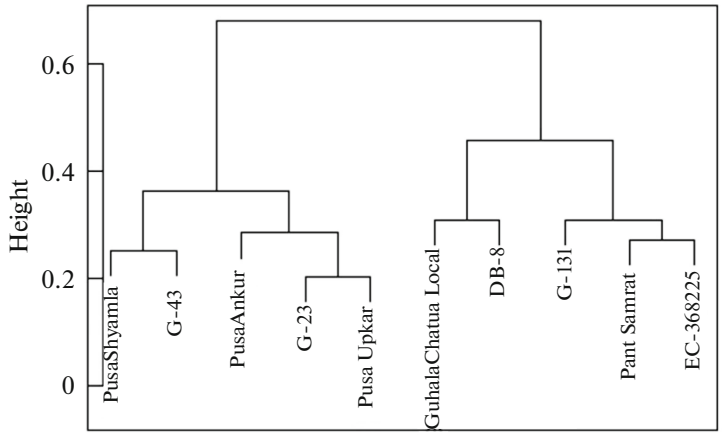


**Fig. 2.** Augmented hierarchical clustering (AHC) based on physiological and biochemical traits among 10 eggplant genotypes under rainy season.

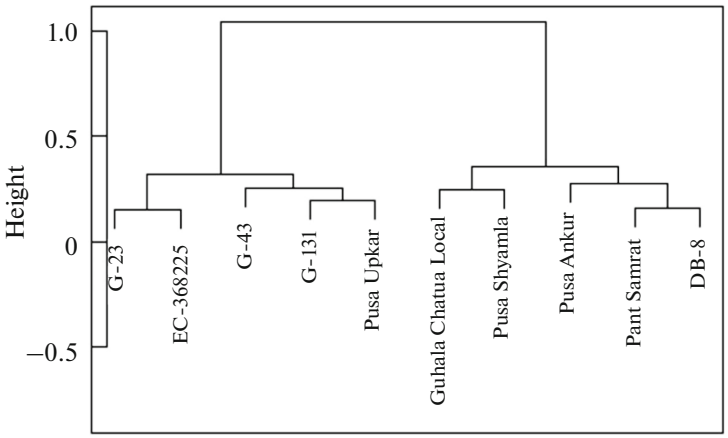


**Fig. 3.** Augumented hierarchial clustering based on physiological and biochemical traits among 10 eggplant genotypes in summer season (under heat stress condition).

*Antioxidant Enzymes and Total Anthocyanin Content*

Antioxidant enzymes (SOD, catalase) and anthocyanin content of both summer and rainy season is represented in Table 5. In summer season, SOD activity was highest in Guhala Chatua Local (41.04 U/min mg protein) and lowest in EC-368225 (29.52 U/mg protein min), with a mean value of 34.69 U/min mg protein. In rainy season, SOD activity ranged from 16.81 to 26.84 U/min mg protein, with an average value of 21.83 U/min mg protein. Similarly, catalase activity was highest in Pusa Ankur (19.06 μmol $H_2O_2$/min g FW) and lowest activity was recorded in G-131 (8.89 μmol $H_2O_2$/min g FW), with a mean value of 13.19 μmol $H_2O_2$/min g FW in summer. During the rainy season, catalase activity ranged from 5.97 to 9.14 μmol $H_2O_2$/min g FW, with a mean value of 7.58 μmol $H_2O_2$/min g FW.

In summer season, the anthocyanin content (TAC) in fruits ranged from 15.67 mg/L in EC-368225 to 655.33 mg/L in Pusa Shyamla, with a mean value of 266.36 mg/L. The anthocyanin in fruits during rainy season ranges from 20.33 to 849 mg/L, with an average value of 381.33 mg/L. The highest and lowest TAC contents were recorded in the G-43 and EC-368225, respectively. The seasonal difference was positive for all the genotypes, and the highest difference was observed for the G-43 (296.33 mg/L).

*Cluster and Principal Component Analysis*

The augmented hierarchical cluster analysis performed on 10 eggplant genotypes is illustrated as a dendrogram in Fig. 2 for the rainy season and Fig. 3 for the summer season. Clustering was performed based on physiological and biochemical traits separately for the rainy and summer season. Based on similarities and dissimilarities, 10 genotypes were grouped into two major clusters. Cluster I comprised of five genotypes, cluster II consisted of 5 genotypes. The dendrogram obtained for the summer season showed two clusters, with five heat stress-tolerant genotypes in cluster II and susceptible genotypes in cluster I.

**Table 5.** Superoxide dismutase, catalase and total anthocyanin content of the summer and rainy season and their seasonal difference (Pooled data)

| Genotypes | SOD, unit/mg protein min | | | Catalase, mmol/g FW/min | | | TAC, mg/L | | |
|---|---|---|---|---|---|---|---|---|---|
| | summer | rainy | seasonal difference | summer | rainy | seasonal difference | summer | rainy | seasonal difference |
| Guhala Chatua Local | 41.04 ± 0.14 | 26.84 ± 2.09 | −14.2 | 15.35 ± 0.61 | 7.21 ± 0.63 | −8.14 | 530.33 ± 16.07 | 720.33 ± 93.00 | +190.00 |
| Pusa Shyamla | 39.49 ± 0.85 | 21.09 ± 0.72 | −18.4 | 14.73 ± 0.41 | 8.40 ± 0.58 | −6.33 | 655.33 ± 29.93 | 837.33 ± 69.57 | +182.00 |
| Pant Samrat | 38.61 ± 0.56 | 20.94 ± 2.51 | −17.67 | 12.58 ± 1.66 | 5.94 ± 0.55 | −6.64 | 116.67 ± 16.80 | 161.67 ± 15.53 | +45.00 |
| DBL-08 | 37.11 ± 3.30 | 22.14 ± 0.87 | −14.97 | 15.37 ± 1.02 | 6.93 ± 0.43 | −8.44 | 139.33 ±15.50 | 194.33 ± 15.30 | +55.00 |
| Pusa Ankur | 32.49 ± 1.44 | 26.58 ± 1.29 | −5.91 | 19.06 ± 1.81 | 8.67 ± 1.15 | −10.39 | 256.00 ±11.00 | 394.33 ± 18.90 | +138.33 |
| G-43 | 32.90 ± 2.46 | 24.62 ± 0.55 | −8.28 | 11.95 ± 1.61 | 9.14 ± 0.63 | −2.81 | 552.67 ±27.57 | 849.00 ± 40.86 | +296.33 |
| G-23 | 30.64 ± 1.30 | 16.81 ± 1.67 | −13.83 | 11.72 ± 1.23 | 8.54 ± 1.30 | −3.18 | 128.33 ±10.01 | 202.67 ± 38.37 | +74.33 |
| EC-368225 | 29.52 ± 0.80 | 18.09 ± 0.79 | −11.43 | 11.69 ± 1.57 | 6.61 ± 0.41 | −5.08 | 15.67 ± 4.10 | 20.33 ± 19.08 | +4.67 |
| G-131 | 34.25 ± 1.41 | 21.32 ± 0.85 | −12.93 | 8.89 ± 0.75 | 5.97 ± 1.59 | −2.92 | 20.00 ±6.55 | 33.33 ± 14.74 | +13.33 |
| Pusa Upkar | 30.89 ± 0.62 | 19.87 ± 0.46 | −11.02 | 10.56 ± 2.15 | 8.43 ± 0.80 | −2.13 | 249.33±38.00 | 398.00 ± 39.73 | +148.67 |
| CDat 5% | 2.92 | 2.38 | – | 2.10 | 0.85 | – | 165.97 | 227.29 | – |
| CV% | 11.78 | 15.28 | – | 22.31 | 15.67 | – | 87.10 | 83.36 | – |

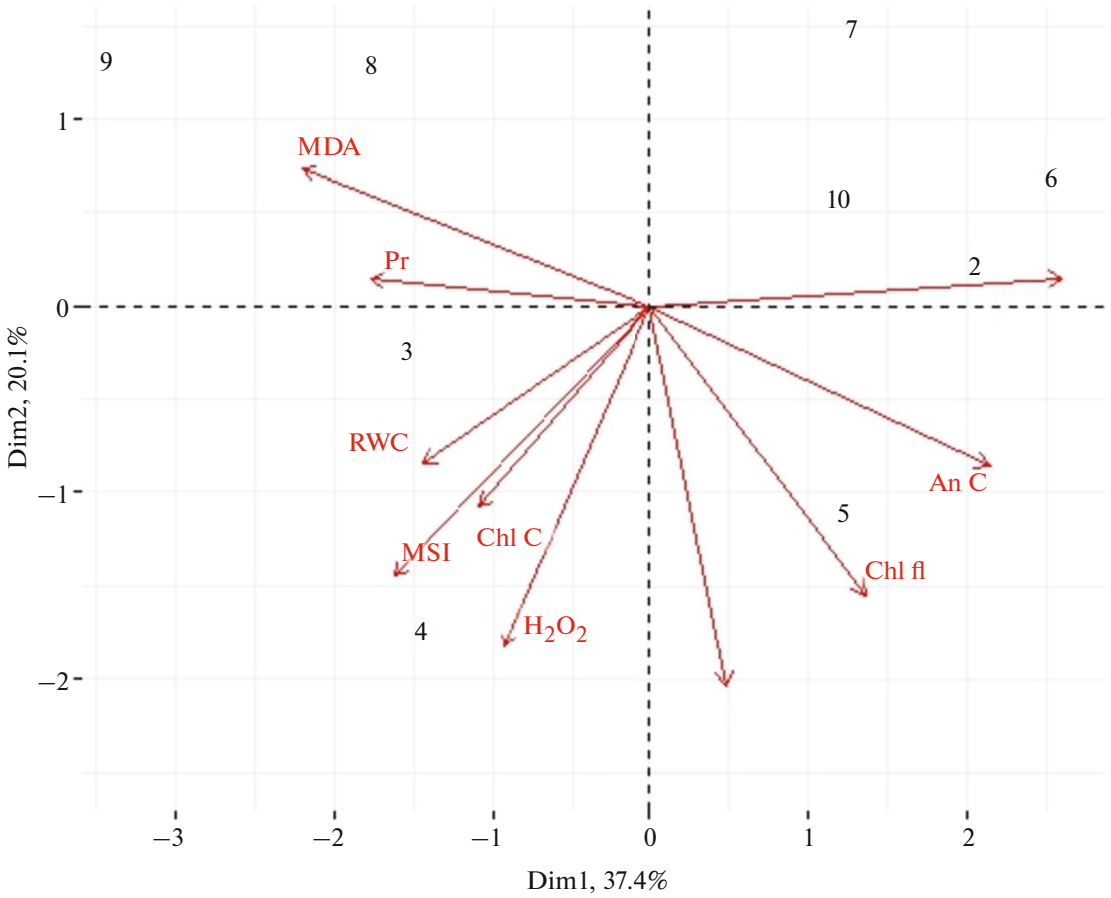


**Fig. 4.** Principal component analysis based on physiological and biochemical traits in 10 eggplant genotypes in rainy season. Genotypes are numbered 1–10 as follows, 1. Guhala Chatua Local, 2. Pusa Shyamla, 3. Pant Samrat, 4. DBL-08, 5. Pusa Ankur, 6. G-43, 7. G-23, 8. EC-368225, 9. G-131, 10. Pusa Upkar. The red lines (arrows) represent the loadings of the traits (variables) on the principal components.

All biochemical and physiological traits were subjected to principal component analysis separately for the rainy and summer seasons, and the resulting biplots are presented in Figs. 4 and 5, respectively. These biplots represent the contribution of variables and individuals towards the variance. Based on the PCA factor loadings, active variables and active observations were grouped into four principal components. The total variance obtained in this PCA was 57.5% for the rainy season and 79.5% for the summer season, respectively. The first principal component (PC1) for the rainy season explained only 37.4% of the variance, whereas for the summer season, it accounted for 64% of the variance in PC1. The lines contributing positively to PC1 in summer season were Pusa Shyamla and Pusa Ankur, indicating its tolerance to heat stresses condition.

## DISCUSSION

In our current study, various physiological and biochemical parameters were estimated under heat stress condition (March–June) when the temperature exceeded 40°C for selected genotypes and a comparative study was conducted with the parameters of crops raised during the normal season (July–October). Reduced water availability is a factor associated with high temperature stress [36]. Similarly, high temperature has been reported to lead the cellular water loss, which in turn retards plant growth as reported in [37]. In our study, among the selected genotypes, the Pant Samrat variety, which had a high RWC value in the summer season, could able to possess tolerance to high temperature than other genotypes. This can be attributed to minimum amount of transpiration loss due to heat stress condition in this genotype. In previous studies, Mazorra and Puneeth [38, 39] found a higher RWC value in heat-tolerant chilli genotypes. A decrease in chlorophyll content was observed at high temperature in tomato [40], mung bean [41], and eggplant [42]. Heat stress has also been found to be associated with premature loss of chlorophyll in many crop species, as reported by Guo et al. [43]. The decrease in chlorophyll was associated with suppressed chlorophyll fluorescence, an indicator of photosynthetic efficiency [44]; these reports indicate that heat stress affects the photosynthetic machinery. Similar to the above-mentioned reports, in the current study, total chlorophyll content and chlorophyll fluorescence

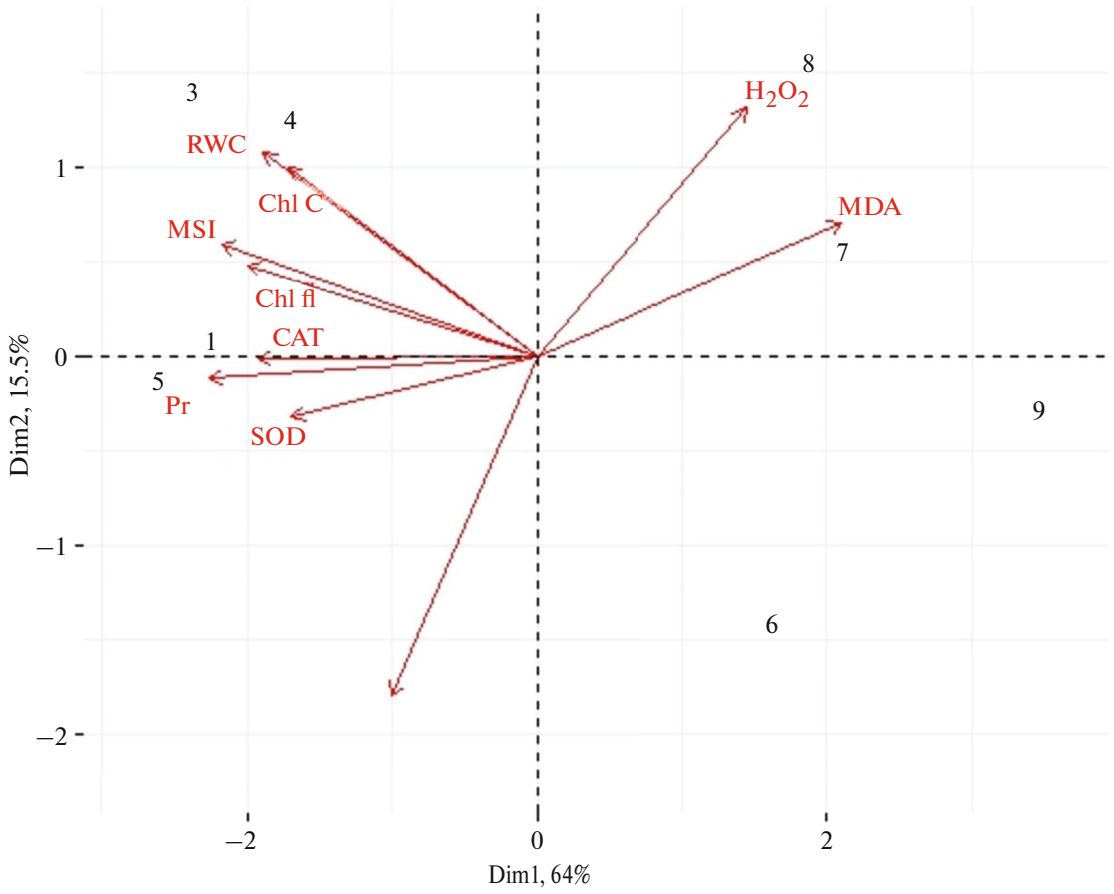


**Fig. 5.** Principal component analysis based on physiological and biochemical traits in 10 eggplant genotypes in summer season under heat stress condition. Genotypes are numbered 1–10 as follows, 1. Guhala Chatua Local, 2. Pusa Shyamla, 3. Pant Samrat, 4. DBL-08, 5. Pusa Ankur, 6. G-43, 7. G-23, 8. EC-368225, 9. G-131, 10. Pusa Upkar. The red arrow lines represent the loadings (variable vectors) of the physiological and biochemical traits included in the analysis.

were found to decrease under heat stress conditions, and Guhala Chatua Local, which possess higher chlorophyll content in the summer season, was considered to be a heat-tolerant genotype, and genotypes with minimum seasonal difference were found to be tolerant to high temperature stress compared to those genotypes showing high seasonal difference. Canopy temperature was less in the tolerant genotype Pusa Shymla, reflecting its ability to reduce canopy temperature through transpiration cooling [45].

Electrolyte leakage from cells is used to calculate the thermo stability index of the cell membrane, which is used to determine the ability of heat tolerance of crops like pepper and wheat [46, 47]. It has been reported that loss of productivity under heat stress is predominantly related to reduced photosynthesis and altered membrane stability [48]. In the current study, stability of cell membrane was comparatively high in Pusa Ankur during the summer season (under heat stress) compared to tolerant genotypes such as G-23 and G-43. A similar report of increased electrolyte leakage under elevated heat stress condition in eggplant was reported by Opoku et al. [49].

In the current study, seasonal differences in hydrogen peroxide content were found to be negative for all genotypes, indicating an increase in $H_2O_2$ production during summer season when the temperature is above the optimum. This result was similar to the results of previous studies reported by Siddiqui et al. [7] for faba bean. Similarly, seasonal difference were found to be negative for all genotypes, which indicate an increase in MDA content under high temperature conditions in summer compared to the rainy season, and overall, higher MDA content was found in susceptible genotypes. A similar finding has been previously reported [50, 51]. The findings indicate that elevated temperatures lead to increase in oxidative stress, leading to lipid peroxidation. Increased production of both MDA and $H_2O_2$ indicates oxidative damage of cells under heat stress, and increased production of these two biochemicals is observed in susceptible genotypes, namely EC-368225, G-131, and Pusa Upkar.

Under high temperature, it was found that there is an increase in proline production in pepper plants [52]. In our study, proline content was high in the tolerant gen-

otype Pusa Shyamla compared to susceptible genotypes such as EC 368225, G-131, Pusa Upkar, and G-23 and G-43 in the summer season. Proline content was higher in summer season compared to the rainy season invariably of genotypes. This result leads to the conclusion that increased proline production play a role in heat stress tolerance. The activity of antioxidant enzymes such as superoxide dismutase and catalase activity was found to be higher in tolerant genotypes during the summer season, which helps in scavenging of free radicals. The seasonal difference was negative in all the genotypes for both the enzymes. Similar responses of SOD activity under heat stress were reported by Rivero et al. [53] in tomato and watermelon. This increased SOD activity helps the genotypes to be heat tolerant [7]. Fu and Huang [54] reported increased activity of catalase enzyme during high temperature conditions, similarly, our current study also supports the fact that there is increased production of catalase, an antioxidative enzyme in summer season especially the rate of production was high in heat tolerant genotypes. Anthocyanins are beneficial to plants, one of the major physiological function of anthocyanin identified recently is its role in antioxidative defence function [55]. In summer season the anthocyanin content is reduced as compared to rainy season in almost all the genotypes. Similar reports sowing decreased trend of anthocyanin production in eggplant under high temperature condition have been reported [55]. The lower value of anthocyanin in summer may be due to breaking of anthocyanin pigment at high temperature. It is interesting to mention that the tolerant lines also rich in anthocyanins which are generally recognized health-promoting properties in modern diets.

Principal component analysis (PCA), a statistical grouping method for dimensional reduction of data [56, 57] was done using physiological and biochemical variables for both rainy and summer season and difference in grouping of genotypes in both the season helped in identifying tolerant genotypes for heat stress condition and variables contributing to its tolerant.

In the present study, it has been found that physiological parameters like relative water content, total chlorophyll content, chlorophyll fluorescence and membrane stability index (MSI) was found higher in rainy season when compared with the summer season this indicates the decline in the above mentioned contents during summer season when the temperature is above optimum for the growth of eggplant genotypes. Canopy temperature was high in summer season than rainy season crop. The seasonal difference in RWC and total chlorophyll content were very minimum in Pusa Shyamla as well as the seasonal difference in chlorophyll fluorescence was minimum in Pant Samrat. Similarly, Pusa Ankur shows minimum seasonal difference in case of MSI. This minimal difference during high temperature condition makes these varieties heat tolerant.

Primary and secondary metabolites play an important role stress tolerance in plants. The production of antioxidants in stressed plants is needed in scavenging reactive oxygen species which affect membrane stability, proteins and nucleic acid in plants [58, 59].

In tolerant genotypes the production of antioxidant enzymes was high than the susceptible genotypes which helps in scavenging the active oxygen species. Proline content generally increases during heat stress condition, Pusa Shyamla, Pant Samrat, Pusa Ankur, Guhala Chatua Local and DBL-08 have higher proline production than the susceptible genotypes which helps them in mitigating the heart stress. Hydrogen peroxide content and MDA content was found to increase during summer season, the rate of increase was high in susceptible genotypes than the tolerant genotypes. Thus, the tolerant genotypes like Pusa Shyamla, Pant Samrat, Pusa Ankur, Guhala Chatua Local and DBL-08 can be further evaluated and can be incorporated in breeding of heat tolerant varieties and can be used to grow in areas were temperature keep above normal during growing season this becomes essential for present days changing climatic conditions.

## ABBREVIATIONS AND NOTATION

| | |
|---|---|
| AnC | anthocyanin content |
| CAT | catalase |
| Chl C | chlorophyll content |
| Chl fl | chlorophyll fluorescence |
| MDA | malondialdehyde |
| MSI | membrane stability index |
| Pr | proline content |
| RWC | relative water content |
| SOD | superoxide dismutase |
| TAC | total anthocyanin content |

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## ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

## CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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